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THE HISTORY OF THE NEOTROPICAL REGION.

IN No. 276 of SCIENCE, April, 1900, Dr. Henry F. Osborn published an article on the 'Geological and Faunal Relations of Europe and America during the Tertiary Period,' to which I may here refer, as it may be useful for science to discuss the different opinions to which our study has led us.

It is singular that Mr. Osborn has no knowledge at all of the numerous papers published by the writer on the history of the neotropical fauna, and consequently it is necessary to say at first some words on these papers, and the new discoveries and ideas published in them. Referring here only to those of my publications in which the geological and zoogeographical relations of South America were fully discussed, I name the following:

1. 'Die Geographische Verbreitung der Flussmuscheln.' *Das Ausland*, Stuttgart, 1890, Nos. 48–49; and translated 'The Geographical Distribution of the Freshwater Mussels.' The New Zealand *Journal of Science*, Vol. I., Dunedin, 1891, pp. 151-154.

2. 'Ueber die Beziehungen der chilenischen und suedbrasilianischen Suesswasser fauna.' *Verhandlungen des deutschen wissenschaftlichen Vereines zu Santiago*, Vol. II., 1891, p. 142–19.

3. 'Ueber die alten Beziehungen zwischen Neuseeland und Suedamerika.' *Ausland*, Stuttgart, 1891, No. 18. Translated, 'On

the Ancient Relations between New Zealand South America.' *Transactions* of the New Zealand Institute, Vol. XXIV., 1891, p. 431–445.

4. 'Die Palaeo-Geographie Suedamerikas.' *Ausland*, Stuttgart, 1893, Nos. 1–4.

5. 'Revision der von Spix in Brasilien gesammelten Najaden.' *Archiv. für Naturgeschichte*, 1890, p. 117–170, Taf. IX.

6. 'Najaden von S. Paulo und die geographische Verbreitung der Suesswasserfaunen von Suedamerika.' *Archiv. für Naturgeschichte*, 1893, pp. 45–140, Taf. III.–IV.

7. 'Das neotropische Florengebiet und seine Geschichte.' *Engler's Botanische Jahrbücher*, Vol. XVII., 1893, pp. 1–54.

8. 'Die Ameisen von Rio Grande do Sul.' *Berliner entomologische Zeitschrift*, Band 39, 1894, pp. 321–446.

9. 'Os molluscos dos terrenos terciarios da Patagonia.' *Revista do Museu Paulista*, Vol. II., 1898, pp. 217–382, Pl. III.–IX., with Conclusions in English, pp. 372–380.

The study of the fresh water fauna, and especially of the Unionidæ of South America, gave me as a practical result the separation of two sub-regions 'Archiplata' and 'Archamazonia.' The first contains Chili, Argentina, Uraguay and Southern Brazil, the second Central and Northern Brazil (Archibrazil) and Guyana, Venezuela, etc. (Archiguyana). Archiplata contains numerous genera of Mollusca, Crustacea, etc., that are common to Chili and the La Plata district, such as *Unio*, *Chilina*, *Parastacus*, *Aeglea*, etc., including many species and even their parasites (*Temnocephala*), which are identical on both sides of the Andes. This contrasts sharply with the Archamazonian fauna, as tropical genera extend to Rio Plata and Rio Negro which are completely wanting in Chili and Peru. In Ecuador, however, the Cordillere form no such zoogeographical division, due certainly to differences in the geological history of both parts of the Andes. For example the Decapod Crustacea in Chili and in the whole of Archiplata are the Parastacidæ and Aegleidæ, but the Potamoninæ are in Archamazonia. Dr. Ortmann has opposed to my explanations the hypothesis that biological differences may be the true reason, exterminating the Potamoninæ that invaded Archiplata, but favoring the Parastacidæ. The observations made by the writer on the biology of these Crustacea emphatically annul the objection. In Northern Argentine, Rio Grande do Sul and St. Catherina, both coexist in the same waters and while the Potamonidæ prefer rivers and brooks, living among aquatic plants, the *Parastacus* selects muddy territory where it can burrow.

That the explanation is a geographical one is proved also by the fact that the species of Unionidæ, Mutelidæ, Ampullariidæ, etc., which occur in the La Plata and in the Rio Paraguay, are almost all Amazonic species. Moreover the faunal relations of the Paraná River are totally different from those of the Paraguay River. In confirmation of these zoogeographical facts the geological ones indicate to us in the Entrerian-formation Unio of the Niæa group, Chilina, Strophocheilus, etc., that is to say, the pure Archiplata fauna. These facts point out that the invasion of the Archamazonian element into Archiplata is quite a recent one. The intrusion of the Archamazonian element is Pliocene or post-Tertiary, and the Andes formed a barrier insurmountable to fresh-water crabs and mussels as well as to fishes, chelonians and alligators.

It is evident that the two faunal elements of South America correspond to geographical districts which were separated by the ocean during the greater part of the Tertiary. The intermixture of the two elements, and especially the intrusion of Bolivian ants, land snails, etc., in Eastern Brazil is by no means finished, but is a fact which

we observe to-day. It is highly probable that these conditions, which are decisive not only for the fresh-water fauna but also for the land gastropods, have determined also the history of the mammals, which may have reached Brazil only in the Pliocene.

Although these inferences concerning the different faunal elements of the neotropical fauna, based on the zoogeographical work of the writer, seem to be quite conclusive, the matter is more difficult and hypothetical if we turn to the ancient relations of Archiplata and Archamazonia to other regions of the globe.

The connection of Archiplata with a great antarctic continent during the Cretaceous and Eocene formation seems now to be generally accepted, but the historic data given on the matter by Osborn are very incomplete. The first to discuss the question was the eminent botanist, Sir William Hooker, but the work of Wallace, and especially his axiom of the permanence of the great oceanic depths, for a long time retarded further progress. Not until 1883 did Hutton, with reference to New Zealand, and in 1890 the writer, with reference to Archiplata, turn aside to publish new facts in favor of the hypothesis of Hooker, which was also confirmed by Fl. Ameghino.

In relation to the ancient connection of Africa and Archamazonia I have given arguments (1890) in favor of a Mesozoic 'archiatlantic continent,' which existed during the earlier Tertiary. At first because of some paleontological facts noted by Schlosser, I believed that this continent could have transmitted Eocene mammals from South Africa to Europe, an idea now defended by Ameghino and Osborn; but in 1893 I modified my opinion and set forth the hypothesis that no Eocene placental mammals had existed either in Archamazonia or in Æthiopian Africa. The ancient continent uniting Archamazonia with Africa I named Archiatlantica in 1890, using in 1892 the term Helenis, and in 1893 that of Archhelenis, with the purpose of preventing confusion with the 'Atlantis' a hypothetical land bridge between South Europe and Central America proposed by Unger.

I will not repeat here what I have said elsewhere as to the intimate relation between the fresh water faunas of Brazil, Guiana, and of equatorial Africa, but I shall make some remarks on the geographical distribution of the fresh-water mussels. North America agrees in its Unionidæ with Eurasia, the genera *Unio*, *Margaritana* and *Anodonta* being predominant. The archiplatic element of South America is formed only by the genus *Unio*, and by a section of it which has no representatives in the holarctic region, forming the subgenus *Nicea*, which is found also in New Zealand and Australia. The numerous presumed genera of *Unio* now admitted in North America all agree in the characteristic sculpture of the beaks, which is quite different in *Nicea*. I consider, therefore, *Nicea* as a genus and the North American sections of *Unio* only as subgenera. In the archhelenic region we have representatives of *Unio* which are more intimately allied to *Nicea* than to *Unio*, no Anodontas, but very numerous representatives of the Mutelidæ. The South American 'Anodonta' are all *Glabaris*, a genus of Mutelidæ allied to *Spatha* of Africa.

Considering the geological history, we find the precursors of the actual North American Unionidæ as far back as the Jurassic period, and what we know of fossil mussels of New Zealand and Archiplata are only *Unios* of the *Nicea* section. On the other hand, Cretaceous deposits of Bahia show us representatives of *Glabaris* and *Mycetopus*. The actual conditions of distribution therefore predominated even in the Mesozoic time, and no explanation can be given of the intimate relation be-

tween the fresh-water faunas of tropical Africa and South America than the hypothesis of an ancient land bridge; supposing that these faunas were only the remains of an ancient cosmopolitan tropical fauna, the paleontological evidence should be totally different.

In regard to the geological distribution of the mammals of South America, the opinions of the respective authors are very divergent. There is, however, one point of which there can be no doubt, *i. e.*, the Pliocene exchange of North and South American types. It must be decided by North American zoologists whether this interchange has commenced at the close of the Miocene or only in the Pliocene. We may therefore consider as Pliocene the Argentine Araucanian formation, where the northern Artiodactyla and other North American immigrants first appear; the Entrerian formation, containing the neotropical forms must then be Miocene. This formation was considered by Ameghino Eocene (1889), or Oligocene (1898), and by the writer (1898), Miocene. In favor of his opinion Ameghino quotes the result of the study of G. Alessandri on the fossil selachian teeth of Entrerios which he believes to be Eocene. Mr. A. Smith-Woodward, to whom I have sent the material of our museum, writes me: "I conclude that the formation cannot be earlier than Miocene and is probably Pliocene." I have called attention to the fact that in the Entrerios deposits occurs *Monophora darwini*, a Scutellid with perforated disk which is common in the corresponding formation of the north Patagonian coast. No Scutellidæ with perforations of the disk are known earlier than the Miocene. On the other hand, the Mollusca of this formation are almost all extinct species and therefore I cannot believe it Pliocene.

Zittel in his 'Manual' has well explained the relations between the two American mammal faunas. I am, however, disposed to believe, contrary to him and to Ameghino, that the genus *Didelphys* in South America appears as a member of the North American immigration. If derived from the Patagonian Microbiotheriidæ, as suggested by Ameghino, this genus may have issued in the earlier Eocene time from Patagonia and Archinotis and, after having reached Europe in the Eocene and North America in the Miocene, turned to South America in the Pliocene. If Ameghino is right, the Proboscidia are derived from the Eocene Patagonian Pyrotheriidæ and, after having appeared in Europe and North America, returned to Argentina during the Pliocene in the form of the Mastodon.

If this migration is a relatively well established fact, it is quite doubtful in what manner Patagonia received its rich mammalian fauna in the Laramie period. Florentino Ameghino pointed out that this must have occurred by means of a land-bridge which united both Americas at the beginning of the Tertiary period. On this matter there has been a discussion between Ameghino and the writer in the *Revista Argentina de Historia Natural*, Vol. I., Buenos Ayres, 1891, p. 122 ff. and p. 281 ff., in which I have combated this hypothesis. The fresh-water faunas of the two Americas, as I have shown, are so completely different that only a prolonged and absolute separation can explain the fact; the geological history of both North and South America demonstrate an enormous development of the Cretaceous Ocean, separating the two Americas, and in the Tertiary period the North American territory increased but slowly. This presumed primitive connection of the two Americas is not at all supported by facts, but only based on the predominance of wrong ideas of the history of the Australasian Territory. The Eocene mammals of Patagonia and North America certainly do not justify this hypothesis. The Eocene faunas of Reims and

Puerco, although these localities are much more distant from each other than North and South America, correspond closely, but the characters of the earliest Tertiary Patagonian and North American mammalian faunas are quite divergent. We find nothing of the Toxodontia, Typotheriidæ and true Edentata in North America, and nothing of the Artiodactyla, Perissodactyla, Amblypoda, etc., in Patagonia. The orders and families which *are* represented in both Patagonia and North America may be such as were distributed over the whole area occupied by placental mammals in the Laramie period.

The third line of migration according to Ameghino and Osborn was determined by the land masses which connected Brazil and Africa. In my papers, and especially in the discussion with Ameghino, I have insisted upon the value of this Eocene land bridge, but I do not believe that it has served for the distribution of mammals, as I believe that Archamazonia was in the greater part of the Tertiary separated by the ocean from Archiplata. In this case Brazil has received mammals only in the Pliocene time, when the communication with Africa had long ago been interrupted. I have examined the deductions of Ameghino and Osborn with the purpose of verifying the facts proving their opinions, but these seem to be very insufficient. Osborn refers to the Pangolins and Aard Varks of the Æthiopian region as introduced from South America 'via Antarctica.' It must, however, be noted that these Edentata of the old world occur also in Asia and that they belong to the Nomarthra, while all the Patagonian representatives are Xenarthra. Both may be derived from a common Australasian ancestor, but if the South African Edentata had been derived from the Patagonian Eocene fauna, they should be Xenarthra. The genus *Orycteropus* occurs also in the Miocene of Samos, and may have immigrated both to Samos and to Africa from its Indo-australian home. It may be observed here that I have shown that the claw of the Dasypodidæ develops in the form of a hoof, and it is wrong to classify the Xenarthra with the Unguiculata, as they are Ungulata. The Proboscidea and Hyracoidea are not Patagonian mammals at all, although in the Patagonian Laramie or Pyrotherium fauna the Pyrotheriidæ and Archæohyracidæ offer relations to the two above-mentioned living families. The case is the same with the sole Patagonian Insectivore, the genus *Necrolestes*, somewhat comparable with the Chrysochloridæ of South Africa. Evidently the few representatives in the Patagonian Eocene of the Insectivora, Prosimiæ and Hyracoidea are the isolated members of groups which were well represented in other regions then in connection with Patagonia. Thus the Chrysochloris argument for the Patagonian-South-African migration is not better than the hypothesis of a land-bridge uniting the Antilles with Madagascar, the sole localities where representatives are found to-day of the genus *Centetes*, which occurs also as Wallace affirms in the European Tertiary.

The intimate relations between the fresh water faunas of Africa and Brazil, and the colossal difference which exists between the fresh water faunas of Archamazonia and Archiplata, prove that both territories during the greater part of the Tertiary were separated quite as completely as the two Americas. In this case the mammalian fauna of Patagonia may have reached Ecuador or Colombia by means of the upheaval of the Andes, but not Brazil, and both Brazil and the Æthiopian region may have been without mammals and especially placental mammals, during the Eocene. When toward the close of the Eocene this land-bridge was submerged, there already existed many types that have been conserved

until our time, and thus we find existing on the Central American and Brazilian coasts the same species of mangrove plants, and with them numerous identical forms of Crustacea, Mollusca, etc.; the distribution of Manatus must also be cited here.

We now turn to the relations of South America with Australia and New Zealand. As the views put forth on this point by Hutton and the writer seem to be now generally accepted, there is no reason for discussing the question here. It may be observed, however, that not only does the fresh-water fauna give evidence of an antarctic land bridge between Australia, New Zealand and Patagonia, but also numerous other zoological as well as botanical and paleontological facts. Osborn says only that this migration established the links with Australia, 'bringing in Marsupials, both polyprotodont and diprotodont.' Ameghino (Censo, p. 250) says that on this vast antarctic land was distributed the cretaceous mammalian fauna which he has described. No other conclusion is logically possible, and we cannot doubt that the Eocene fauna of the Australian region, though not at all known to-day, must have been very analogous to and in part identical with the Patagonian.

The different adaptive radiations of orders and families have given a very different aspect to the existing faunas of Australia and Patagonia, in Australia only Monotremates and Marsupials having survived, in Patagonia principally histricomorph Rodents and Edentata. The existing fauna of Australia, New Guinea and other allied islands has received by Miocene immigration some placental mammalia, as *Canis* and *Uromys* in Australia, *Sus* and *Uromys* in New Guinea, and other genera in the Moluccas. This proves that Australia and New Guinea, at least during the Miocene, continued to be connected with Asia as in the foregoing periods. There existed therefore in the earlier Tertiary a continuous land mass from Antarctica and Patagonia, via Australia and Asia, to Europe and North America. This enormous territory, my Eurygæa, was the birthplace of the placental mammals. The Stenogæa (or Archhelenis) extending from tropical South America to Africa, Madagascar and Bengal was in the Eocene without mammals.

It is certain that we have to-day no knowledge at all of the Eocene mammals of Australia, Brazil and Africa, but from the facts given it seems to be highly probable that future discoveries may confirm what we expect.

Paleophytical studies have given evidence of a great resemblance between the Cretaceous floras of North America and Eurasia. According to Fr. Kurtz, the same flora appears also at St. Cruz, Patagonia em Cerro Guido (*Revista Museu La Plata*, Vol. X., 1899, p. 43 ff.). According to the facts given above, this flora cannot have reached Patagonia from North America, as the two Americas were then separated and no South American continent existed. It is also impossible to admit that a land bridge formed by the Andes served for the migration, because these did not then exist, as the Cretaceous marine beds of the Andes prove. There must then have been a connection between the Antarctic Cretaceous continent, the Archinotis of the writer, and Asia. It may be observed that the genus *Quercus* was represented in the Cretaceous beds of both Patagonia and Australia, where to-day it has no representative. What has occurred in the case of *Quercus* and other genera in both Australia and Patagonia and what is observed in Patagonia with reference to mammals may have happened also in Australia to the earlier placental mammals. Further, it must be remembered that Australia, and South America also, developed by coalescence of different parts, each of which had its own history.

I may note here one more fact referring to the fresh water fauna: the dispersion of the cyprinoid fishes. These Holarctic fishes did not reach Australia, already isolated by the sea, but invaded Africa and Madagascar. Lemuria must therefore have persisted in connection with Asia, when the Australian region was already isolated. Thus Africa offers the same mixture of ancient indigenous elements and Neogene immigrants as Argentina and Southern Brazil, on account of the intrusion of archamazonic immigrants. Had this invasion occurred in the Eocene period, the Cyprinidæ would have reached Brazil; supposing it to be Pliocene, these fishes would not have reached Madagascar. Probably Africa received its placental mammals at the same time that the invasion of Cyprinidæ into Africa took place, one of the most remarkable events in zoogeography.

We have no knowledge at all of the Cretaceous and Eocene mammals of Brazil, Guyana, Africa and Australia; it is impossible to give a complete history of the mammals with incomplete materials. But combination of the known facts makes it probable that during the Cretaceous and Eocene period Archhelenis, or Stenogæa, was without placental mammals and that their origin was in Eurygæa. In regard to the flora the same holds good for many families of wide distribution, as for example the Cupuliferæ.

With reference to the terms used by Blandford, Lydekker and the writer, it must be said that the intention of the first two was to give names to *existing* zoogeographical regions, while the terms introduced by me refer to *supposed, ancient* zoogeographical and geographical regions. The two great Cretaceous continents Eurygæa and Stenogæa may have existed also during a part of the Eocene period and then dismembered. From Stenogæa, or Archhelenis, were separated first Bengal and then Madagascar, while Archamazonia after the loss of the connection with Africa consisted of Archiguyana and Archibrazil. Eurygæa split into (1) Archiboreas corresponding to the actual holarctic region and (2) Archinotis from which, in the Eocene, Archiplata was separated.

The comparison of the distribution of the mammals with the fresh water fauna makes especially evident the differences in the geographical conditions which must have determined their distribution. While the distribution of the existing types of mammals is a result of changes in geography during Tertiary time, the most fundamental facts in the distribution of the fresh-water fauna dates from the Mesozoic epoch. The fresh-water fauna of Chili preserved such a remnant of the Cretaceous fauna almost intact, and even the connection between the two Americas has not at all modified the South American fresh-water fauna. On the other hand, representatives of the Archamazonian fauna, in correlation with the geographical modifications of Central America and the Antilles have invaded the southern parts of the nearctic region. Thus in the Rio Usumacinta of Mexicao beside Cyprinidæ and Chromidæ we find also Characinidæ and Lepidosteus, also species of *Glabaris* intermediate between the northern Unios and Anodontas. There is a further difference in the distribution of mammals and fresh-water mussels. The former migrate on land bridges in both directions, the fresh-water fauna generally in only one, due to the opportunity given by the currents. Thus although there was an invasion of Cyprinid fishes into Africa there was no corresponding emigration of Æthiopian types. A similar fact is the sudden appearance of the Æthiopian faunal elements in the valley of the Nile, which occurred only at the close of the Pleistocene, as proved by paleontological facts. While the Pliocene connection of the two Americas was sufficient to mod-

ify the distribution of the mammals in such a way that without paleontological researches it would be impossible to recognize the origin of the different faunal elements, the fresh-water faunas have resisted almost unchanged all modifications in the configuration of the continent.

The fresh-water fauna is not only older but also much more conservative than the distribution of the mammals. One of the most striking examples of this is given by the history of Africa. While the characteristic mammals are Neogene immigrants and Lydekker proceeds quite correctly in making Africa an annex only of the Holarctic region, thus establishing his Arctogæa, with relation to the fresh-water fauna, Africa is a part of South America, somewhat modified by the Neogene invasion of Cyprinid fishes. If as regards mammals Africa belongs to Arctogæa, with relation to the fresh-water fauna it belongs to the Archhelenic region.

This example demonstrates *the absurdity of the present system of construction of zoogeographical regions and maps. We can construct maps of the different classes and orders but not at all of the animal kingdom, because the geological history of the different groups is quite different.* When Osborn says that it is one problem 'to connect living distribution with distribution of past time,' he says only what had been the leading idea of Wallace and of Engler in their eminent works on zoo- and phytogeography, but when he continues 'and to propose a system which will be in harmony with both sets of facts,' he proposes a problem just as contradictory as would be the construction of descriptions and figures referring at the same time to egg, larva, nympha and imago of an insect. The works on 'zoogeography' are almost exclusively discussions of the distribution of mammals and birds, and the few words spent on other classes are only ornamental supplements. A wrong method cannot give valid results. For the exploration of the zoogeographical relations and regions of the beginning of the Tertiary and of the preceding Mesozoic epoch it is necessary to study and to discuss the more ancient classes and, as I have insisted for ten years, principally the fresh-water fauna.

H. von Ihering.

São Paulo, July 20, 1900.

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*A HISTORY OF THE DEVELOPMENT OF THE QUANTITATIVE STUDY OF VARIATION.**

The quantitative study of variation has for its object the investigation of evolution by exact, quantitative methods. The study demands a mathematical method as well as a biological subject matter; consequently the development of the science has proceeded along two main lines—the one biological and the other mathematical. Accordingly, the history of the development of the quantitative method involves a consideration of both the study of variation and the elaboration of the necessary method.

The fact of variation has been recognized since man began to think and to appreciate that in stature, color and mental capacity his fellow-men are diverse. The way for quantitative studies in biology was paved by the mathematical studies on the variation of measurements which engineers and astronomers found it necessary to make for their own purposes. These mathematical studies led to the discovery and elaboration of the law of error by Gauss and others—and this law is the corner-stone of the quantitative biological studies.

The application of the law of error to organic variation was, apparently, first made by an anthropological statistician, of the early part of the century, named Quetelet. In his book, entitled 'Lettres à Son Altesse Royale le Duc de Saxe-Coburg et

* Being part of the report of the Committee of the American Association for the Advancement of Science on the Quantitative Study of Variation.